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Title:

A DETERMINATION OF THE EFFECTS OF FOLIAGE QUALITY ON LARVAL DENSITY AND
LEVEL OF DEFOLIATION OF DOUGLAS-FIR TREES BY WESTERN SPRUCE BUDWORM

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FINAL REPORT: 1979 WSB - Douglas-fir study conducted near Boulder, Montana

Activity

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SUMMARY:

The major objective of this investigation was to identify possible foliage quality characteristics which have an effect on the population dynamics of the western spruce budworm. The objective was to be accomplished through multiple correlation analysis between several foliage quality and tree growth characteristics with the current year's larval density.

Results indicated that trees with large amounts of myrcene, cadinene isomer, and two unknown terpenes tended to have fewer number of budworm growing on them. Trees whose terpene production went to the synthesis of high molecular weight compounds tended to be more resistant to budworm. Additionally, the distribution of terpenes within a tree proved to be highly correlated with density. Trees whose terpene distribution varied greatest ^{from?} for the overall population's terpene distribution were less susceptible to infestation.

Density of what?
Insects or trees/acre

INTRODUCTION

Foliage quality is an important factor in the population dynamics of the western spruce budworm (WSB) and is a primary determinant in the resistance-susceptibility characteristics of Douglas-fir trees at endemic and epidemic larval populations (Heron, 1965, Wilkinson, 1970, Cates and McMurray, 1978, and McMurray, 1980). The major objective of the present investigation is to determine how WSB density is correlated with the foliage quality characteristics of Douglas-fir trees. Emphasis was placed upon determining the relationships of variation in nutritional and resistance-susceptibility characteristics (i.e. heritable tree characteristics which reduce the probability of successful utilization of that tree by WSB) of Douglas-fir trees to WSB density. This objective was to be accomplished by investigating the following questions:

- 1) Do some Douglas-fir trees have foliage quality characteristics (as defined by total nitrogen content, monoterpene concentration and composition, resin acid content, tannin content and polyphenol content) which increase their resistance to WSB larvae by reducing the density of budworm attacking the foliage?
- 2) Do larvae reared on resistant trees grow more slowly than those reared on more susceptible trees? Are adults from larvae reared on resistant trees smaller and lower in fecundity than those on more susceptible trees?
- 3) Is there an inverse correlation between larval growth, density and fecundity and various foliage quality characteristics of Douglas-fir trees?
- 4) Can trees be assayed quickly with regard to their degree of resistance to WSB for incorporation into silvicultural management programs?

METHODS AND EXPERIMENTAL DESIGN:

I. Site Selection, Density, Defoliation, Growth and Fecundity Measurements:

A. Site Selection:

Studies on the resistance-susceptibility characteristics of Douglas-fir in Montana began in May, 1979. The research site selected was approximately five miles south-east of Boulder, Montana, in the Deer Lodge National Forest. The area selected consisted of a monoculture of Douglas-fir trees with an occasional ponderosa pine, juniper and lodgepole pine. The site was selected after consultation with John Hard, Jed Dewey, and Larry Stipe (all of Region 1) and David Fellin and Clint Carlson (Forestry Sciences Laboratory, Missoula, Montana). The site was also selected on the basis of information passed on from reviewers through program management. Budworms have been present in this general area for about 10 years (Johnson and Denton, 1975, personal communication, Region 1 foresters, 1979). The current budworm population was not declining and was considered to be healthy.

Initially 147 trees were tagged of which about 80 were used in the experimental work described below. The area of the site was approximately 1.5 square mile⁵. Careful consideration was given to reducing the variability among trees within the site by selecting trees with a similar age, height, bole radius, and crown diameter. Trees were also selected such that they were growing in similar microenvironments (proximity to drainage, angle and attitude of slope, and distance to neighboring trees). Two to three weeks were spent in locating sites.

B. Budworm Density Measurements:

Natural budworm density on the trees was measured by sampling six sprays at midcrown in the same quarter of the tree that was used for foliage quality analysis. Sprays were clipped using an 18 foot pole cutter. Once clipped, the sprays and any dislodged larvae were caught using a large blanket placed directly under the branch being sampled. Each spray was 40 cm long. The number of budworm and

number of buds were counted for each spray. An average larval density was calculated for each tree. Budworm density was measured during the third to sixth instars. Density is expressed as the average number of larvae per 100 buds per tree.

C. Defoliation Measurements:

A visual estimate of defoliation was made for all trees based on the amount of remaining foliage on the entire tree. Trees which had less than 30% of their foliage remaining were classified as being highly defoliated. Trees with 30% to 70% of their foliage remaining were classified as being moderately defoliated, while trees with more than 70% of their foliage remaining were classified as being of a low defoliation level. The percent foliage remaining on each tree was determined by three independent observations each of which corroborated one another. Each defoliation level was assigned a coefficient as follows: Highly defoliated = 3, moderately defoliated = 2, and a low level of defoliation = 1.

D. Larval Growth and Fecundity Measurements:

Larval growth and fecundity measurements were not made. Second instar larval emergence was late during the spring of 1979. The information used to initially schedule the sampling period for larval growth and fecundity measures was incorrect by about 2-3 weeks. Unfortunately, this delay did not allow the collection of the larval growth and fecundity measures. (See Problems Encountered section)

II. Tree Measurements, Foliage Collection and Chemical Methods:

A. Tree Measurements:

The following tree growth parameters were measured and used to determine their relationship to the dependent variable (budworm density): age (determined by tree cores), crown diameter, bole radius (both determined using a metric tape), height (determined by triangulation) and date or time of bud burst (verified every three days). In total, approximately one week was spent taking tree measurements.

B. Foliage Collection:

[Approximately] fifteen to twenty-five grams of the current year's foliage was collected at mid-crown level in the same quarter that the density measurements were taken. Foliage samples were kept on ice until they could be frozen. Foliage samples for monoterpene analysis were collected concurrently and encapsulated in indium tubing as described in section C.

C. Chemical Methods:

1) Polyphenol measurements:

Polyphenol content (mg/g needle tissue) was determined by homogenizing 5 g of the current year's foliage in 70 ml of 70% acetone containing 1g/l L-ascorbic acid and 0.2g/l NaCN at 4°C. L-ascorbic acid was used to prevent oxidation while NaCN was used to prevent enzymatic breakdown. The homogenate was filtered and washed with 30 ml of 70% acetone until the total volume was brought up to 100 ml. Excess NaCl was added to the extract to increase the ionic strength of the water which results in the separation of the water and acetone into two layers. The polyphenols are forced into the upper acetone layer due to the ionic concentration of the water. The acetone layer was pipetted off and evaporated to 40 ml. Eighty mls of ethanol and 200 ml of diethyl ether were added to the acetone. In ethanol the polyphenols become insoluble and precipitate. Fifty ml of diethyl ether were added to the precipitate, mixed thoroughly, and the precipitate was allowed to settle. This is done to clean impurities from the extract. Polyphenolics are not soluble in diethyl ether. The supernatant was pipetted off for the second time. The precipitate was vacuum dried and dialyzed in distilled water. This is to remove any complexed or associated salt which may have precipitated out with the polyphenolics. The distilled water was replaced at hourly intervals until the water gave a negative reaction to AgNO_3 , a test for soluble NaCl. At this point polyphenols were dried

and weighed. This amount represents the total polyphenol content for the sample. The polyphenols were then solubilized in 6.2 mls of 20% acetone and evaporated down to 5 ml. Four ml of gelatin solution (15 mg gelatin/4 ml H₂O) were added along with 3 ml buffer (29.4 g/l sodium citrate lowered to pH 5 with HCl) and maintained at 20°C for 2 hours. The solution was centrifuged at 3000 rpm for 10 min, washed with buffer, and finally dried to a constant weight at 60°C. The residue was weighed and tannin weight was derived from the standard curve of tannin versus the tannin protein-complex. This method of tannin and polyphenol analysis was used because it yielded a total polyphenol content as well as a tanning coefficient. Other methods traditionally use spectrophotometric methods which have problems with differential molar absorbtivity. The method used here is gravimetric and avoids such problems.

2) Total nitrogen determination:

Total nitrogen was determined by standard microkjeldahl digestion of 250 mg dried plant material with subsequent analysis on an auto-analyzer. The nitrogen determinations were contracted to Dr. James Gosz's laboratory at the University of New Mexico.

3) Monoterpene determination:

Samples were prepared for gas chromatographic analysis by slicing 4 mm midsections out of 5 needles weighing usually 15-25 mg, and then encapsulating the midsections in indium tubing in the field. A Cahn electric millibalance (sensitive to 0.01 mg) along with a 12 v converter were used such that sample preparation could be performed in the field using a 12 v car battery. After encapsulation, the samples were stored at -20°C. Encapsulation was performed to prevent volatilization of terpenes.

The frozen solid samples (15.0-25.0 mg) of needles encapsulated in 0.120 inch OD x 0.080 inch ID x 1 inch indium tubing were placed in a stainless steel boat and

then sealed in a splitter injector set at 190°C . The gas chromatograph is a Perkin-Elmer 3920B equipped with flame ionization detectors. The column was a 0.10 inch x 150 foot capillary packed with 85% OS-138, 14% CO-880, and 1% V-930 by Perkin-Elmer. Helium flow was set at 0.5 ml per min. Temperature programming was as follows: 32 min at 70°C , an increase of 8°C per min to 170°C , then 38 min at 170°C . Standards were used to identify alpha-pinene, beta-pinene, beta-phellandrene, camphene, 3-carene, limonene, bornyl acetate, myrcene, citronellyl acetate, and geranyl acetate. Compounds for which standards are unavailable and hence are unknown were assigned an identification number according to their retention times. As more standards become available, we hope to eventually be able to identify these unknown compounds. The concentration of each compound (known or unknown) was determined as integrator counts per gram fresh weight. The total amount of terpenes in the tissue, expressed as counts per gram fresh weight was calculated by summing all known and unknown compound concentrations for that particular sample. The sample chromatograph was also divided into three equivalent sections according to retention time: the low molecular weight fraction with a relatively short retention time, the intermediate molecular weight fraction with a relatively longer retention time, and the high molecular weight fraction with the longest retention time. Compounds with short retention times may function differently with respect to affecting larval physiology, and hence budworm larval survival and density, than compounds with long retention times since the functional groups of the fractions differ.

Additionally, the diversity of terpenes and the difference between an individual tree's terpene diversity and the population's average terpene diversity were also calculated. The diversity index used was the Shannon-Wiener index of diversity, $H = -\sum p_i \log p_i$, where p_i = the relative proportion of terpene P_i .

Because each tree possessed the same number and kinds of terpenes, differences in the diversity value (H-Diff) merely reflected differences in the evenness of distribution of the quantities of the individual terpenes. H-Diff demonstrated whether terpenes in a particular tree were more or less evenly distributed than the population average.

4) Resin Acid Determination:

Tissue for resin acid determination was sent to D. F. Zinkel, Forest Products Laboratory, Madison, Wisconsin for analysis.

III. Statistical Analyses:

Measurements of thirty-one parameters were used as independent variables in the multiple stepwise correlation (Table 1). The combining of alpha-pinene and camphene was done since on most chromatographs they were difficult to separate. Terpene diversity, H, was not used at all in the analysis. This is because H is strongly correlated with H-Diff ($r=-1.00$), and one is just the inverse of the other. Therefore, both cannot be used in a multiple correlation analysis. Resin acid content and concentration were not used in the analysis, because no detectable resin acids were found in the tissues sent to Dr. Zinkel.

The dependent variable correlated with the above independent variables was the "corrected" average larval density. This variable was calculated by multiplying the average larval density per 100 buds per tree by the defoliation coefficient for that tree. The corrected average value was used because of the problem involved in a one-time sampling of larval density as a measure of the degree of resistance or susceptibility of any given tree. Corrected larval density takes into consideration the movement of larvae from highly defoliated trees due to a lack of suitable foliage. In severely defoliated trees, measurements of larval densities may underestimate actual damage done to the

tree, because at high defoliation levels larval migration takes place due to larval starvation (Morris, 1963). Therefore, when corrected larval density was used the effects of previous years' defoliation was accounted for.

Multiple correlation analysis was performed to determine the relationship between the above foliage quality and tree growth characteristics and corrected average larval density of the western spruce budworm on each tree. Analysis was performed using an BMDP program on an IBM 360 computer. This analysis was used to determine the order of importance of each independent variable upon the dependent variable, and the importance of each on budworm density.

10/4/82
What bothers me about this analysis is the dependent variable. It is at least 50% defoliation, and defoliation, it seems to me, would greatly affect foliage chemistry. If it does, then we have a circular argument -- tree chemistry affects insect populations, and insect populations affects defoliation, and defoliation affects chemistry. In my mind, you need to study foliage chemistry on trees with no defoliation and then establish the insect response.
Russ Mitchell

RESULTS AND DISCUSSION:

I. Results:

Of the 30 independent variables used, 12 explained 53.7% ($R^2 = 0.537$) of the total variation (Table 2). Height, stress index, total nitrogen content and the combined concentration of alpha-pinene and camphene showed a positive relationship with the corrected average larval density. Bole radius, time of bud burst, the high molecular weight fraction of the chromatograph, myrcene, unknown terpene 6, unknown terpene 10, cadinene, and H-Diff are all inversely correlated with the corrected average larval density, suggesting that these variables may confer resistance to the trees.

Examination of the standardized correlation coefficient of the twelve significant variables (Table 2) showed H-Diff, stress index, the high molecular weight fraction, and the combined concentrations of alpha-pinene and camphene as being the most important variables in predicting the budworm density on a tree. Cadinene, total nitrogen content, height, and myrcene were of a relatively moderate importance in predicting budworm density. Unknown terpene 10, bole radius, time of bud burst and the unknown terpene 6 were the least important in predicting density.

Partial correlation coefficients (the correlation between a single individual independent variable and the dependent variable, holding all other variables constant) indicated a pattern similar to the standardized correlation coefficients. Variables with the strongest partial correlation were H-Diff, myrcene, total nitrogen and stress index. The combined concentrations of alpha-pinene and camphene, bole radius, unknown terpene 10, and time of bud burst were moderately correlated with density. Height, the unknown terpene 6, cadinene isomer, and the high molecular weight fraction of the chromatograph had the smallest partial correlation with density.

*What's stress index?
I didn't see that measurement
in the methods section.
Pg 10*

What's meant

II. Discussion:

According to the standardized correlation coefficients, H-Diff is the most important single variable in predicting budworm density. This suggests that the more uneven an individual tree's terpene composition becomes, relative to the population's average (i.e. the larger H-Diff becomes), the more resistant the tree may be to WSB. Since H-Diff was calculated using relative abundance of terpenes, the importance of H-Diff in the analysis further implies that the relative distribution of terpenes within a tree is important in determining resistance. Specifically, the more even the relative distribution of terpenes becomes, the more resistant to budworm a particular tree will be. Although H-Diff does not indicate which terpenes or groups of terpenes are responsible for the increasing unevenness, other variables in the analysis indicate which compounds may be responsible for this relationship. The absolute quantity of cadinene, a high molecular weight compound, was negatively correlated with corrected average larval density (std. regr. coef. = -0.293). Additionally, susceptible trees exhibited high concentration of the alpha-pinene and camphene fraction. That the above compounds are those responsible for the changes in evenness was corroborated by examining trends in mean values for those compounds among trees grouped by defoliation level. (Table 3). The means for myrcene, unknown terpene 6, unknown terpene 10, cadinene, and the high molecular weight fraction of the terpene chromatograph were all higher in resistant trees while the mean for the combined value of alpha-pinene and camphene was essentially the same in the two groups.

These data suggest that a tree has a limited amount of energy to use for terpene production. Resistant trees seem to use most of their energy available excess for terpene synthesis in the production of the relatively high molecular weight compounds. This is not to say resistant trees do not place any emphasis on the production of the lower molecular weight compounds. Myrcene and unknown terpenes

Not exactly; there is some evidence that trees have a priority system for allocating the products of photosynthesis. Some primary production is required before carbohydrates can be given to non-essentials such as resin & terpene production.

6 and 10 are all of less importance than cadinene or the high molecular weight fraction of the chromatograph.

Total nitrogen content was positively correlated with corrected average larval density. This is not surprising since nitrogen is often a limiting factor in an herbivore's diet. Therefore, trees with a higher nitrogen content should be more susceptible to attack. Trees with a lower nitrogen content will tend to be less suitable for WSB growth and hence more resistant. It should be noted that nitrogen may be toxic at high nitrogen levels (McMurray, 1980; Wayne Brewer, pers. commun.). This was not found to be the case in this study.

Corrected average larval density was negatively correlated with time of bud burst. The development of WSB is closely related to tree phenology. Therefore, factors that cause a delay in the time of bud burst may result in less defoliation and less budworm success. Interestingly, delay of bud burst seems to be the most important factor in conferring resistance in black spruce to the eastern spruce budworm (Morris, 1963).

The stress index (tree age/height) was positively correlated with budworm density. This suggests that the more stress a tree is under, the greater the density of budworms infesting the tree. Bole radius, a measure of tree vigor and productivity, was negatively correlated with budworm density. That is, the more vigorous and healthy a tree, the fewer the number of budworm larvae on the tree. Bole radius and stress index are likely both a measure of overall tree vigor. Both lead to the conclusion that a stressed tree is more likely to be more heavily infested than a healthy productive tree.

Tree height was positively correlated with corrected average larval density. This relationship is difficult to explain. Height has traditionally been a measure of vigor. In this study, however, inverse relationships exist between height and bole radius with corrected average larval density. One possible explanation would be that a tree which is extremely tall, has put most of its

Height is not a measure of vigor; height/age is a measure of site productivity. Height by itself is just height.

Any explanation? WSB? This one of his? Shredders?

or what survives? This tells nothing about vigor; it must be related to age to suggest vigor. Even that doesn't say much about current vigor.

implies too much

I question this as being stress. It's just site index (a measure of productivity) and around.

available energy into growth and little into chemical defense. Therefore, extremely tall trees may be more susceptible to larval attack. This relationship has yet to be proven.

It should be noted that resistance is related to the population dynamics of the budworm. That is the greater the population size, the more likely that even a resistant tree, as measured at endemic levels, might succumb to the enormous population of budworms. The data presented in this report suggest, however, that at even high densities, Douglas-fir trees may maintain a high level of resistance thereby reducing the budworm density significantly in comparison to those trees that are susceptible.

CONCLUSIONS:

The above data and interpretations are consistent with previous studies conducted in New Mexico using Douglas-fir tussock moth and western spruce budworm in that foliage quality of the host does have an adverse effect on the budworm. Research conducted in 1977 on the Douglas-fir tussock moth-white fir interaction suggests that white fir foliage quality is an important factor in determining the degree of resistance or susceptibility to DFTM (McMurray, 1980). Larval preference studies conducted in the laboratory, using foliage and larvae collected in the field from the Sangre de Cristo mountains, New Mexico, indicated a significant variation in the resistance of individual trees to DFTM. Larval preference decreases (tree resistance increases) with increasing levels of alpha-pinene, camphene, bornyl acetate and total amounts of terpenes (Table 4). When DFTM are raised in the field at endemic levels on young needles of white fir (Sangre de Cristo site), larval growth was shown to be inversely correlated with levels of camphene, limonene, bornyl acetate and total amount of terpenes (Table 5). This inverse relationship with larval preference and growth suggests these compounds may be active in conferring resistance in white fir to DFTM.

Research conducted in 1978, has shown similar patterns with the western spruce budworm-Douglas-fir interaction. Adult female dry weight decreased with increasing total nitrogen and bornyl acetate, and increased with decreasing amounts of an unknown minor terpene, terpene 10 (Table 6) (McMurray, 1980). In this case, high levels of nitrogen adversely affected female dry weight which was not the case in the Montana study reported here. Additionally, adult male dry weights were shown to decrease with increasing concentrations of camphene, bornyl acetate, myrcene, unknown high molecular weight terpene (terpene 11), and total terpenes (Table 7) (McMurray, 1980). These inverse relationships suggest that

these compounds in the foliage of Douglas-fir may confer resistance to WSB.

(Please note the numbering of unknown terpenes was unique to each study).

The current study, indicates that myrcene, cadinene, two unknown terpenes, and the high molecular weight compounds are inversely related with corrected average larval density. These data suggest that these compounds, or groups of compounds, may be partially responsible for conferring resistance in Douglas-fir to WSB under epidemic insect levels. This is consistent with the preceeding studies that also show inverse relationships between specific mono-terpene content and various insect parameters (Table 8). The inverse correlations between larval density and stress index or bole radius suggest that healthy, productive trees are less susceptible to heavy budworm infestation. The combined concentration of alpha-pinene and camphene as well as the total nitrogen content of the foliage were positively correlated suggesting that these variables may in fact be cues used by the budworm to locate susceptible trees.

*What this means?
Trees change in terpene content?*

The change in correlation from previous years; research (1978) between total nitrogen content and the combined concentrations of alpha-pinene and camphene with larval density may be explained by taking into account the stage that the budworm population was in at the time (of foliage and insect and sampling). Previous studies (1978) were conducted on sites which were supporting endemic levels of budworm. The current study was conducted on a site which has been under heavy infestation for several years. This budworm stress seems to have resulted in the production of high levels of nitrogen, probably in the form of amino acids. It is not suprising that budworms larvae might respond positively to increasing levels of nitrogen. At high concentrations, however, amino acids are known to be toxic to several herbivores (Brewer, et al, 1980). *What stress?*

In addition, it should be pointed out that this study could not detect factors which may have conferred resistance to the trees prior to the time of outbreak. It may be that under high density budworm levels, Douglas-fir prod-

If that's true, then we need a different study design. It seems to say regardless of what we find

uces an induced defensive system different from the system employed at endemic levels. This cannot be determined until trees are sampled at endemic levels and a determination of the resistant mechanism(s) compared to those in high level budworm populations. The current data do suggest that despite high levels of infestation, Douglas-fir trees do exhibit resistance to WSB as measured by decreased larval density.

RECOMMENDATIONS:

Additional research is needed using agar diets to determine which of the terpenes are responsible for adversely affecting the budworm. The mechanism of action of these potential toxins also needs to be elucidated. It is important to note that these compounds may only be markers of resistance and may not be the actual compounds conferring resistance. Agar diet studies, scheduled to begin in our laboratory in 1981, would satisfy some of these questions. Determining the foliage quality of Douglas-fir at different geographical locations across the western U.S. and how these different foliage qualities affect the associated endemic or epidemic budworm populations would be invaluable. Questions such as how variable and effective are foliage quality characteristics from area to area could be ascertained. To a certain extent this work is already being carried out. Foliage quality analysis has already been performed on one site in Montana, a site in Idaho, and three sites in New Mexico. Additionally, a study which follows the changes that may occur in the foliage quality of Douglas-fir as an associated WSB population expands from endemic to epidemic levels is needed. Such a study ^{may clarify} would elucidate if resistance mechanisms are inherent, inducible, or if such mechanisms change with changes in the status of the insect population. The implications are strong from the data gathered that foliage quality characteristics can and do effect larval population dynamics, but it is not known if larval population dynamics influence foliage quality characteristics. Investigations pursuing these ideas need to be continued and refined. Following a basic understanding of the above, several management techniques could be determined such as planting a wide diversity of trees relative to their defensive chemistries in areas which have been defoliated by western spruce budworm.

back To The old
(but sound!) idea
of diverse species comp.
to reduce insect attack?
To reduce susceptibility?

WORK REMAINING ON STUDY:

The current study was completed. This report is being modified for publication in Environment Entomology or a forestry journal.

COOPERATION AND COORDINATION:

We wish to thank those scientists of Region 1 for their help before this grant was funded and their continued advice during the selection of sites. John Hard, Larry Stipe, and Jed Dewey were extremely helpful as was David Fellin and Clint Carlson (INT Forest and Range Exp. Sta.). A special thanks to David Fellin for the time he spent showing Cates several potential research sites. We wish to extend our thanks to Dr. D. Zinkel for his analysis of Douglas-fir foliage for resin acids.

PROBLEMS ENCOUNTERED:

The only major problem encountered was that of late resumption of larval activity. Information supplied to us suggested great variability in larval emergence in western Montana making it difficult to determine actually when budworm larvae would begin feeding on young foliage. Budworm emergence was actually 2-3 weeks later than expected on our site in 1979. Since the study was budgeted to support a field crew for only a limited time, the late emergence of WSB created severe time and financial constraints. As a consequence, the rearing of larvae was abandoned. Unfortunately, there is no good method for predicting weather and its affects on larval activity. The resulting problems due to this were unavoidable.

MANUSCRIPTS OR REPORTS/PREPARED OR PLANNED:

This report is being modified appropriately for publication in Environmental Entomology. It will be submitted for publication in about 2 months with Timothy McMurray, Rick Redak, and Colin Henderson as junior authors.

Table 1. Independent variables used in the multiple stepwise correlation analysis.

CHEMICAL VARIABLES

Concentration of:

alpha-pinene

beta-pinene

camphene

myrcene

limonene

borneol

geraneol

citronellol

bornyl acetate

citronellyl acetate

cadinene

alpha-pinene and
camphene

4 unknown terpenes (hydrocarbons & alcohols)

total terpenes

the high molecular
weight fraction of chromatograph

the moderate molecular
weight fraction of chromatograph

the low molecular
weight fraction of chromatograph

H-Diff

polyphenol content

tannin content

total nitrogen content

TREE GROWTH VARIABLES

age

height

stress index (=age/height)

bole radius

crown diameter

time of bud burst

why not defoliation too?

The greater numbers means more stress?

Why does Rex insist on Bole Radius
vs. DBH? - how do they relate?

Table 2. Summary of multiple correlation analysis using corrected average larval density as the dependent variable.

Analysis of Variance Table

Source	Sum of Squares	df	Mean Square	F-ratio
Regression	3253.498	12	271.125	4.74 ($p < 0.01$)
Residual	2801.427	49	57..72	

Summary Statistics

Multiple R: 0.733

Multiple R^2 : 0.537

Intercept: -10.782

Variable in Equation	Coefficient	Std. Error of Coefficient	Standardized Correl. Coefficient	Partial Correlation
Height	0.664	0.357	0.282	0.256
Bole radius	-1.365	0.620	-0.235	-0.300
Stress index	2.949	1.133	0.337	0.348
Time of Bud Burst	-2.118	0.968	-0.229	-0.298
Total nitrogen content	6.226	2.367	0.285	0.352
High molec. wt. fraction	-0.099	0.059	-0.310	-0.232
Myrcene	-0.043	0.018	-0.276	-0.368
Terpene 6	-0.357	0.197	-0.208	-0.251
Terpene 10	-0.288	0.132	-0.249	-0.298
Cadinene isomer	-0.537	0.313	-0.293	-0.238
Alpha-pinene and camphene	0.014	0.006	0.301	0.300
H-Diff	-55.715	15.421	-0.562	-0.459

Table 3. Means of terpene (integration counts/g fresh weight needle) concentrations for trees grouped by defoliation levels.

<u>Terpene</u>	DEFOLIATION LEVEL		
	Low	Moderate	High
Myrcene	62.40	37.68	29.34
Terpene 6	3.45	3.44	2.09
Terpene 10	3.61	5.53	1.44
Cadinene	9.82	5.43	5.88
Alpha-pinene & camphene fraction	216.40	284.27	217.19
High molec. wt. fraction	62.15	40.59	33.38

Table 4. Relationship of per cent needle tissue eaten (dependent variable) by Douglas-fir tussock moth larvae to the terpene content in young needles of white fir trees (Sangre de Cristo site). (McMurray, 1980)

Independent Variable	Slope	$\pm$ 95% C.I.	Units	Significance Level ^a
α -Pinene	- 9.1253	8.6652	arc sin $\sqrt{\%$ eaten/(ul/g)	<0.050**
Camphene	-36.7593	31.6389	"	<0.025**
β - Pinene	- 4.6001	5.8393	"	<0.100
Limonene	-24.1216	27.3906	"	<0.100
bornyl Acetate	-13.6592	8.9933	"	<0.005**
Total Terpenes	- 0.0048	0.0042	arc sin $\sqrt{\%$ eaten/(counts/g) ^b	<0.050**

a Linear regression, H_0 : slope = 0

b Counts = terpene peak area integration

** Significant at the 0.005 level

n = 52

Table 5. Relationship of Douglas-fir tussock moth larval live weight (dependent variable) to the terpene content in young needles of white fir trees (Sangre de Cristo site). (McMurray, 1980)

Independent Variable	Slope	$\pm$ 95% C.I.L	Units	Significance Level ^a
α -Pinene	- 9.8417	16.5254	mg/ (μ l/g)	< 0.250
Camphene	-80.8259	52.7389	"	< 0.005**
β -Pinene	- 7.6992	10.3331	"	< 0.250
Limonene	-54.4375	49.8630	"	< 0.050**
Bornyl Acetate	-26.9657	13.3755	"	< 0.001**
Total Terpene	- 0.0009	0.0008	mg/(counts/g) ^b	< 0.050**

a Linear regression, H_0 : slope = 0

b Counts = terpene peak area integration

** Significant at the 0.05 level

n = 25

Table 6. Relationship of western spruce budworm female adult dry weight (dependent variable) to the chemical constituents of young needles and the xylem pressure potential of Douglas-fir trees (south Jemez site). (McMurray, 1980)

Independent Variable	Slope	$\pm$ 95% D.I.	Units	n	Significance level ^a
Water Potential	- 0.9984	1.0536	mg/-bars	116	< 0.100
α -Pinene	2.4766	3.2467	mg/(μ l/g)	73	> 0.250
Camphene	- 8.6916	14.5133	"	73	< 0.250
μ -Pinene	11.4637	12.7163	"	73	< 0.100
Myrcene	*	*	"	73	*
Limonene	- 7.3792	19.3032	"	73	> 0.250
Bornyl Acetate	14.6639	13.8622	"	73	< 0.050**
Isoborneol	*	*	mg/(counts/g) ^b	73	*
Terpene 7	*	*	"	73	*
Terpene 8	- 0.0299	0.0362	"	73	< 0.250
Terpene 10	+ 0.0444	0.0396	"	73	< 0.050**
Terpene 11	- 0.0113	0.0305	"	73	> 0.250
Terpene 13	- 0.0189	0.0202	"	73	< 0.100
Total Terpenes	- 0.0002	0.0003	"	73	> 0.250
Total Nitrogen	9.5458	8.3280	mg/% dry weight	115	< 0.050**
Soluble Nitrogen	- 7.2953	16.6621	"	110	> 0.250
Polyphenols	0.2169	0.2257	mg/% fresh weight	103	> 0.100
Tannins	- 5.1103	7.9389	"	104	> 0.250

a Linear regression, H_0 : slope = 0

b Counts = terpene peak area integration

* F-level insufficient for computer computation of slope, $\pm$ 95% C.I., and significance level

** Significant at the 0.05 level

Table 7. Relationship of western spruce budworm male adult dry weight (dependent variable) to the chemical constituents of young needles and the xylem pressure potential of Douglas-fir trees (south Jemez site). (McMurray, 1980)

Independent Variable	Slope	±95% C.I.	Units	n	Significance Level ^a
Water Potential	- 0.0380	0.4185	mg/-bars	118	> 0.250
α-Pinene	- 4.4378	4.5278	mg/(μl/g)	72	< 0.100
Camphene	8.9850	8.3996	"	72	< 0.050**
β-Pinene	- 6.3536	7.7074	"	72	< 0.250
Myrcene	23.4209	21.9583	"	72	< 0.050**
Limonene	- 7.0011	10.0558	"	72	< 0.250
Bornyl Acetate	10.6360	8.3408	"	72	< 0.025**
Isoborneol	*	*	mg/(counts/g) ^b	72	*
Terpene 7	*	*	"	72	*
Terpene 8	- 0.0196	0.0217	"	72	< 0.100
Terpene 10	- 0.0038	0.0235	"	72	> 0.250
Terpene 11	0.0208	0.0156	"	72	< 0.010**
Terpene 13	*	*	"	72	*
Total Terpenes	0.0002	0.0002	"	72	< 0.050**
Total Nitrogen	0.7646	3.9807	mg/% dry weight	108	> 0.250
Soluble Nitrogen	4.8355	6.5137	"	104	< 0.250
Polyphenols	0.0212	0.0928	mg/% fresh weight	99	> 0.250
Tannins	0.8540	2.4778	"	94	> 0.250

a Linear regression, H_0 : slope = 0

b Counts = terpene peak area integration

* F-level insufficient for computer computation of slope, ±95% C.I., and significance level

** Significant at the 0.05 level

Table 8. Summary of results from previous and current research.

<u>SITE</u>	<u>INSECT</u>	<u>DEPENDENT VARIABLE</u>	<u>HOST</u>	<u>SIGNIFICANT INDEPENDENT VARIABLE</u>	<u>CORRELATION</u>
Laboratory Studies, 1977					
Field collected foliage	DFTM	% needle tissue	white	alpha-pinene	negative
and larvae. Sangre de Cristo,		eaten	fir	camphene	"
NM, 1977 ^a				bornyl acetate	"
				total terpenes	"
Sangre de Cristo, NM, 1978 ^a	DFTM	Larval live	white	camphene	negative
		weight	fir	limonene	"
				bornyl acetate	"
				total terpenes	"
South Jemez, NM, 1978 ^a	WSB	female adult	Douglas-	bornyl acetate	negative
		dry weight	fir	unknown terp. 10	positive
				total nitrogen	negative
South Jemez, NM, 1978 ^a	WSB	male adult	Douglas-	camphene	negative
		dry weight	fir	myrcene	"
				bornyl acetate	"
				unknown ter. 11	"
				total terpenes	"
Boulder, MT, 1979	WSB	corrected	Douglas-	height	positive
		average larval	fir	bole radius	negative
		density		stress index	positive
				time of bud burst	negative
				total nitrogen	"
				high molec. wt.	"
				myrcene	"
				unknown terp. 6	"
				unknown terp. 10	"
				cadinene isomer	"
				alpha-pinene & camphene	positive
				H-Diff	negative

^a McMurray, 1980

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